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Before and after wasting disease in common eelgrass *Zostera marina* along the French Atlantic coasts: a general overview and first accurate mapping

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ABSTRACT: We examined the original manuscripts of a French national survey conducted in 1933 on the state of common eelgrass *Zostera marina* beds along the French Atlantic coasts during the period when wasting disease struck the entire North Atlantic population in the 1930s. Based on GIS related techniques and old sets of aerial photographs, we present the first accurate mapping of the *Z. marina* beds before wasting disease occurred and assess their spatial recolonization since the 1950s in the Chausey Archipelago (France), which contains large *Z. marina* beds. The national survey confirmed that the *Z. marina* beds almost totally disappeared from the French coasts during the 1930s. However, the disease symptoms seem to have begun locally a few years before. On the study site, we found that the *Z. marina* beds were more than twice as extended than as they are today, and covered both subtidal and intertidal areas. By the 1950s, 20 yr after the onset of the disease, the beds had hardly recolonized, and contrary to the recolonization patterns reported elsewhere in Europe, they were mainly restricted to subtidal areas. The subtidal and intertidal *Z. marina* beds on the site are now rapidly expanding.

KEY WORDS: *Zostera marina* · Common eelgrass · Wasting disease · Long-term change · Accurate mapping · France

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INTRODUCTION

Wasting disease has been responsible for most of the decline of common eelgrass *Zostera marina* populations in the North Atlantic, affecting all populations in the 1930s (Rasmussen 1977, den Hartog 1987). In addition to the numerous debates about the cause of this disease (for reviews see Rasmussen 1977, den Hartog 1996), other questions concerning this phenomenon are still outstanding.

It is generally accepted that the disease was very significant, striking 90 % the North Atlantic population of the species (Muehlstein 1989), and occurred from 1931

in North America and 1932 in Europe (den Hartog 1987). However, only a few documented cases allow us to assess how significant this disease was over large scales (e.g. the level of degradation of the beds over an entire country). Interestingly, some historical data also revealed that wasting disease-like damage patterns were recorded before the 1930s (den Hartog 1989).

Moreover, the state of the beds before the disease occurred is poorly known (den Hartog 1987). Because of the scarcity of older documents, the scientific community is still uncertain about the former areal extent of the beds, and their former bathymetric positions. The map of Oudemans et al. (1870) of the Dutch Wad-

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den Sea is probably the oldest map of *Zostera marina* beds known to exist before the disease struck, and is followed by maps from 1901 in Denmark (Boström et al. 2003). In France, the only pre-disease map of *Zostera* beds was published by Joubin (1909) of the Roscoff area, and sketches were made by De Beauchamp & Lami (1921) of Bréhat and by De Beauchamp (1923) in the Ile de Ré. In Germany, Nienburg (1927) performed a rough seagrass distribution map (*Z. marina* and *Z. noltii*) of the Königsbay (Sylt) in 1924 (Reise et al. 1989).

A few authors used these old data to study in more detail the ecology (de Jonge & Ruiter 1996) or the evolution of the beds before and after the disease occurred. Den Hartog & Polderman (1975) and de Jonge & Ruiter (1996) used the data of Oudemans et al. (1870) on the Wadden Sea, Blois et al. (1961) and Jacobs (1979) used the data of Joubin (1909) in France, Reise et al. (1989) used the data of Nienburg (1927), and van der Heide et al. (2007) used the 1931 map of Reigersman et al. (1939). However, these older documents have to be used with great caution for several reasons. First, there is a risk of confusion with other *Zostera* species; for example, Joubin (1909) mapped all the *Zostera* beds, mixing the 2 species (*Z. marina* and *Z. noltii*) so that the distinction between the 2 species *a posteriori* can be hazardous. Second, these older documents did not allow accurate mapping, and they can be difficult to compare with mapping based on aerial photographs. Also, the estimations of superficies can be difficult, especially when it comes to distinguishing different bathymetric levels covered by the beds. Thus, additional calculations were required to determine the extent of error (see de Jonge & Ruiter 1996). Finally, studying the spatial patterns of recolonization of the beds before and after the disease on a particular site is all the more interesting because the site has not been strongly affected by anthropogenic activities. The western Wadden Sea radically changed after the closure of the Zuyderzee. It was subjected to significant, but not well documented, increases in turbidity, eutrophication and fishery activities (den Hartog & Polderman 1975, de Jonge & Ruiter 1996, van Katwijk et al. 2000, de Jonge & de Jong 2002, van der Heide et al. 2007).

Up to now, the earliest maps of *Zostera marina* beds performed through photo-interpretation in Europe have been those made in 1932 by Glémarec et al. (1996) of the Glénan Archipelago in France during the time when the wasting disease occurred. However, a large part of their study area was hidden by cloud cover and, thus, many photos were not optimally usable. Consequently, no accurate spatial reference state of the Atlantic seagrass beds has been produced since before the 1930s. To study the temporal changes

in the eelgrass stands we used a French national survey of 1933 and a series of aerial photographs available from the years 1924, 1953, 1982, 1992 and 2002.

In this paper we aim to (1) assess, on a large scale, the dates of the first occurrences of wasting disease along the French coasts and the level of degradation of the beds, and (2) accurately assess for the first time the spatial evolution and the bathymetric position of the *Zostera marina* beds before and after the disease, and their current state in a site hosting large beds of the species where anthropogenic pressures during the 20th century have been minor.

MATERIALS AND METHODS

On 13 March 1933, a French military ministerial dispatch was sent to each district of the Affaires Maritimes about the disease affecting *Zostera marina*. We explored all the original manuscripts currently stored in the French Museum of Natural History. Eight questions were addressed, but here we focused on only two: (1) 'Are the seagrass beds of your region in a worse state than in the past? Are they totally or partially destroyed?' and (2) 'When did the disappearance or the decline of the eelgrass of your region begin?' Because we noticed some confusion between the 2 species, *Z. marina* and *Posidonia oceanica*, found in the Mediterranean districts, we only dealt with data from the 82 districts of the Atlantic and the English Channel coasts.

Five aerial photographic mosaics were assembled with 5 sets of aerial photographs taken of the Chausey Archipelago in Normandy, France (Fig. 1) in the following years: 1924, 1953, 1982, 1992 and 2002. All the *Zostera marina* beds were mapped on a 1:1000 scale with Arcview 3.1 Software at each date. The extents of the beds at different bathymetric levels were calculated with GIS by intersecting the different layers corresponding to a bathymetric map (extracted from Tocquet et al. 1957) and the mapped *Z. marina* beds.

RESULTS

The national surveys revealed that almost all the *Zostera marina* beds of the French Atlantic coast and of the French–English Channel coasts partially or totally disappeared (Fig. 2). The disease occurred mainly in 1931 ($n = 23$ districts) and 1932 ($n = 14$), but also as late as 1933 ($n = 2$). More surprisingly, occurrences of the disease were also recorded as early as 1930 ($n = 6$) and even before that ($n = 12$) (Fig. 2).

In 1924, the *Zostera marina* beds of the Chausey Archipelago covered 763 ha (Fig. 3). Though they

occurred mainly on shallow subtidal areas (51 %), they ranged from deeper subtidal areas (13 %) to intertidal sandflats (36 %). In 1953, 20 yr after the first occurrence of wasting disease, the beds barely covered 8 % of their 1924 area (60 ha), and were essentially restricted to subtidal areas (84 %). The recolonization continued

from 1953 to 2002, mainly in shallow subtidal areas, but the beds also extended to intertidal and deeper subtidal bathymetric levels. The development of the *Z. marina* beds was particularly important between 1992 and 2002 when the extent of the beds increased by 92 %. In 2002, though the bathymetric range of the beds was almost the same, they were still only half as extensive as they were in 1924 (Fig. 3).

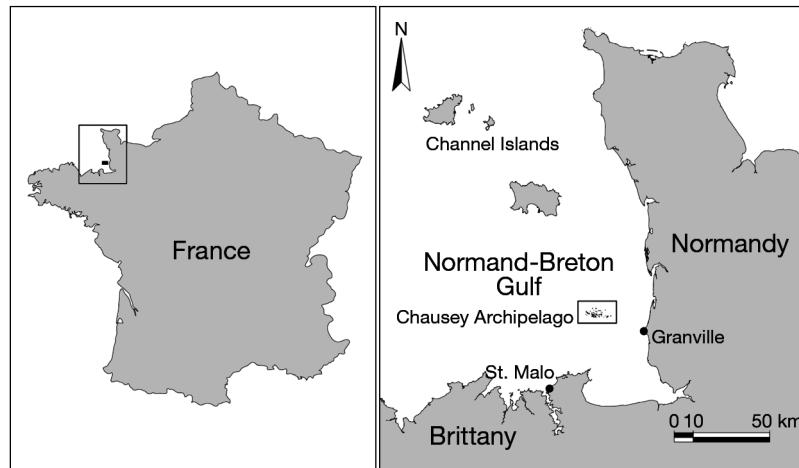


Fig. 1. Study site on the north coast of France. Expanded inset shows location of Chausey Archipelago in the Norman-Breton Gulf

DISCUSSION

A significant outbreak emerges before 1932

The 1933 French national survey showed that almost all the *Zostera marina* beds along the French coast (except along the Mediterranean Sea) were totally destroyed. This is important to know when looking at present day sites where the largest *Z. marina* beds exist, such as the Bassin d'Arcachon and the Golfe du Morbihan (Fig. 2).

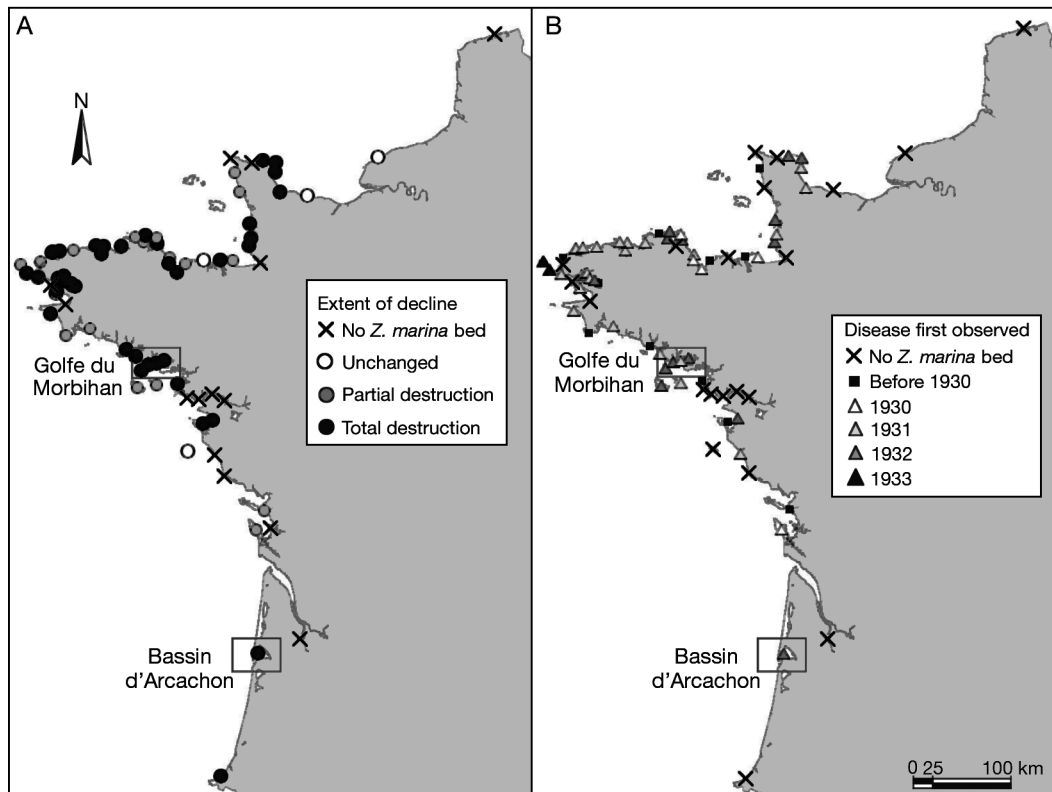


Fig. 2. *Zostera marina*. (A) Level of destruction of the eelgrass beds and (B) dates of the observation of the disease according to the survey of 1933. Boxed areas indicate location of largest present-day eelgrass beds

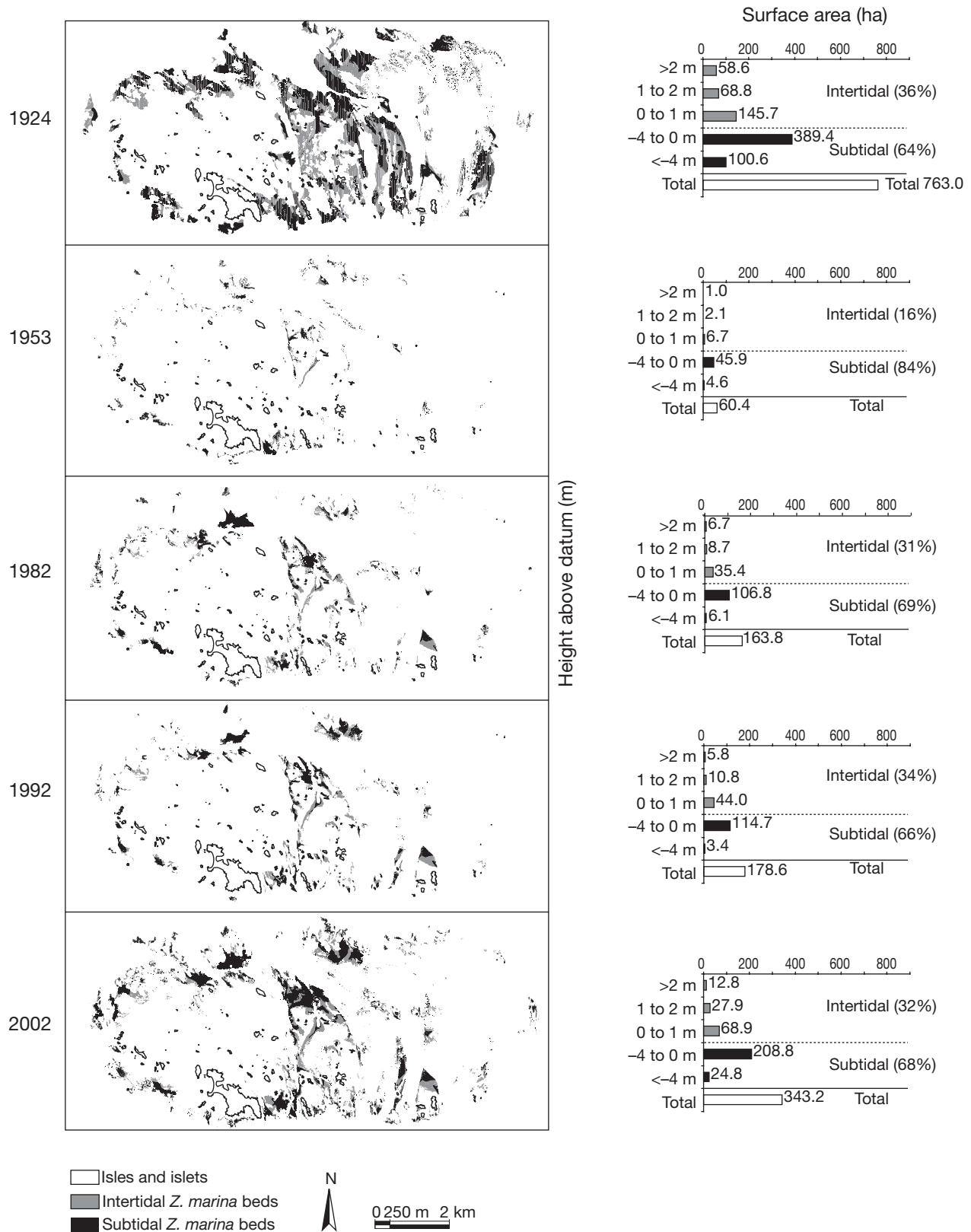


Fig. 3. *Zostera marina*. Spatial evolution of the eelgrass beds of the Chausey Archipelago since 1924. Datum (0 m, dotted line) in histograms: extreme low water (spring tide)

The results of the 1933 survey confirm the ubiquity of the seagrass decline related to wasting disease observed elsewhere in North America and in Europe, where large beds totally disappeared. For example, in May 1932, all the *Z. marina* beds in the Dutch Wadden Sea were struck suddenly, and in a few days almost all beds had been infected and had died (den Hartog 1996).

Wasting disease is known to have occurred in 1931 in North America and in 1932 in Europe (den Hartog 1987), or around that same time period (Rasmussen 1977). This is partially confirmed by the 1933 survey. Nevertheless, the survey also reveals frequent reports of the disease occurring before 1930, as suggested by a few others. In Great Britain, Butcher (1934) recorded that *Zostera marina* beds had not been doing well since 1920. Early records of wasting disease-like damage before 1930 were also reported by den Hartog (1989) for the British Isles and The Netherlands when he studied herbarium materials of the British Museum and the Rijksherbarium of The Netherlands. As suggested by den Hartog (1989, p. 223), this may reveal that wasting disease is 'an inconspicuous, but widespread endemic phenomenon, normally occurring in eelgrass beds.'

A slow recolonization from subtidal areas

The 760 ha of luxurious *Zostera marina* beds of the Chausey Archipelago in 1924 had hardly begun to recolonize by 1954, and only reached 8% of their original surface area, essentially restricted to subtidal areas. We assume that they had almost totally disappeared between these 2 dates, probably between 1931 and 1932, as recorded in the national survey for this particular region (Fig. 2). Moreover, Lami (1933) reported that *Z. marina* beds were almost absent from the site in 1933, and even the large beds of more than 100 ha had not yet recovered by 1937 (Lami 1937). The time lag before recolonization began was long. Similar situations were also assessed in France in the 1950s. In the Glénan Archipelago, the *Z. marina* beds were scarce in 1952 and only began to improve in the 1970s (Glémarec et al. 1996). In 1957, the *Z. marina* beds around Roscoff were also scarce, and the recolonization really begun in the 1960s (Jacobs 1979). Elsewhere in Europe, the recovery was also very slow and *Z. marina* beds were still absent in a number of areas by 1951 to 1953 (Rasmussen 1973). In the Danish coastal waters, Frederiksen et al. (2004) observed a time lag of at least 10 yr before recolonization began. In the Wadden Sea, subtidal beds never recovered, because turbidity related to suspended sediment was too high,

probably because turbidity was no longer reduced by seagrass itself (positive feedback, van der Heide et al. 2007). Intertidal *Z. marina* beds in the Wadden Sea fluctuated considerably between 1932 and 1965, further declined during the 1970s (den Hartog & Polderman 1975), and stabilised at 'near absent' levels in The Netherlands and at low levels in Germany since the 1990s (Reise et al. 2005, see www.zeegras.nl).

However, there is an important difference between the recolonization patterns of the *Zostera marina* beds of the Chausey Archipelago and those of other sites in Europe. In the Chausey Archipelago, recolonization was restricted to subtidal areas in 1953. In contrast, Jacobs (1979) concluded that the intertidal populations of *Z. marina* in the Roscoff vicinity were hardly affected by the disease. In The Netherlands, the *Z. marina* beds had been largely confined to subtidal areas before the disease occurred (van der Heide et al. 2007), but they only remained in intertidal and brackish areas after the disease was established (den Hartog & Polderman 1975). In Devon, England, Wilson (1949) reported that the wide-leaved sublittoral *Z. marina* was replaced by a more narrow-leaved intertidal form, and this has not changed since (den Hartog 1987). These reports from other locations in Europe suggest a recolonization pattern from intertidal or brackish areas, which has been partly explained by an 'annual strategy' of these beds (den Hartog 1987). The intertidal recolonization patterns versus the subtidal ones we observed in the Chausey Archipelago can be explained in 3 ways.

(1) Until now, data about the recolonization patterns of the *Zostera marina* after the disease have been anecdotal. Thus, it is still difficult to draw general conclusions over a large scale about any recolonization pattern either from subtidal or from intertidal areas. The few data only allow for site-by-site observations, and each observation has to be considered as a particular case.

(2) In the Chausey Archipelago, the optimal habitat conditions of *Zostera marina* correspond to shallow subtidal waters, where the species has been the most abundant over the 20th century, whereas in the Dutch or English coasts they correspond to intertidal areas and brackish waters. Consequently, the *Z. marina* beds only recolonize from their optimal living conditions areas after the disease has gone. However, this hypothesis differs from the results of Jacobs (1979) and Blois et al. (1961) who observed that recolonization patterns develop from intertidal areas, which are less affected by the disease, in the Roscoff region (160 km from Chausey), where the optimal living conditions of the species may be similar to those of the Chausey region.

(3) The optimal habitat living conditions are subtidal, but recolonization may be more difficult in subtidal areas. This may be caused by 2 mechanisms or a combination of both: (a) the 'K-strategy' of the subtidal beds in comparison with the 'r-strategy' of the intertidal beds that colonize easily (e.g. Jacobs 1982), and (b) because light may be limited in subtidal beds after the disappearance of the plants as the plants may contribute to the local reduction of water turbidity, and low light levels occur particularly in turbid, eutrophic or otherwise affected areas like the UK or Dutch coasts (de Jonge et al. 2002).

Present changes in *Zostera marina* beds: Does global warming matter?

Large scale losses of *Zostera marina* beds have been recorded around the world in recent decades, and can largely be attributed to anthropogenic causes (Short & Wyllie-Echeverria 1996, Orth et al. 2006a,b), although none, as yet, have been as catastrophic as that caused by the wasting disease of the 1930s (Short et al. 1986, 1988, 1993, den Hartog 1994). However, declines were also reported on sites where anthropogenic effects are considered to be minor, such as in the Glénan Archipelago beginning in the 1980s (Glémarec et al. 1996). Glémarec et al. (1996) blame the 2 declines of the 1930s and those from the 1980s on global warming, following one of the hypotheses of Rasmussen (1973, 1977) who evoked a warming climate as a potential reason for the breakdown of *Z. marina* in Europe in the 1930s. Conversely, the *Z. marina* beds of the Chausey region have been developing in the last 2 decades, and particularly quickly since 1992. This is strongly contradictory to the global warming hypothesis. The long-term change of the *Z. marina* beds analysed in this paper suggests that the *Z. marina* beds are currently recovering in the colonized areas lost since the occurrence of wasting disease. This recolonization has been accelerating over the last decade, which is probably only due to a 'self accelerating process' (Hemminga & Duarte 2000), related to positive feedbacks (see Duarte 1995, Munkes 2005, Bernard et al. 2007, van der Heide et al. 2007). Thus, we can suppose that at other sites in Europe and North America, the rapid development of human activities along the coasts is more likely to be the cause of the regression of the *Z. marina* beds than is global warming. Locally, human activities may also have positive effects on *Z. marina* beds development, as recently reported in the Ems estuary, The Netherlands, where the geomorphology dramatically changed due to the disposal of harbour sludge (de Jonge & Brauer 2006).

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